Ciliary Feeding Assisted by Suction From the Muscular Oral Hood of Phoronid Larvae

R. R. STRATHMANN[1] AND Q. BONE[2]

[1]*Friday Harbor Laboratories and Department of Zoology, University of Washington,*
620 University Road, Friday Harbor, Washington 98250; and [2]*Plymouth Marine Laboratory,*
Citadel Hill, Plymouth PL1 2PB, Great Britain

Abstract. Phoronid larvae have an oral hood upstream from a postoral encircling array of ciliated tentacles. Cilia move water over the hood and between the tentacles, from anterior to posterior. When an algal cell or other particle in this current contacts a tentacle, the neighboring part of the hood lifts, and the particle is drawn toward the mouth. The correlation between movements of hood and particles indicates that the particle moves with water entering the enlarged space beneath the hood. Each lift of the hood is preceded by contact between a particle and a tentacle. A hood lift follows contact with a particle anywhere along the length of a tentacle, and clearance rates are thus proportional to the total length of tentacles deployed and the velocity of the current past the tentacles. After being detained at the ciliary bands of tentacles, particles are transported by the hood lift at speeds exceeding measured transport along the frontal ciliated surfaces of other larval forms. Faster transport may aid capture of faster prey. The larva's feeding mechanism is unique to the phylum Phoronida. Larvae of brachiopods, bryozoans, hemichordates, and echinoderms have similar ciliary bands producing feeding currents, but none are known to transport food toward the mouth by suction produced by muscle contractions.

Introduction

The actinotrocha is the feeding larval form of the lophophorate phylum Phoronida. There is conflicting evidence on homologies between structures of the actinotrocha and those of other larval forms. The actinotrocha resembles the deuterostome larvae of hemichordates and

echinoderms in the arrangement of the ciliary bands of its tentacles and in its monociliate cells (Garstang, 1962; Strathmann, 1973; Zimmer, 1973; Herrmann, 1976; Nielsen, 1987; Lacalli, 1990). Less obviously, it resembles spiralian trochophores and differs from deuterostome larvae in the direction of beat of preoral cilia on the margin of the oral hood (Lacalli, 1990). A close relationship between phoronids and spiralians has also been inferred from studies of 18s ribosomal DNA sequences (Halanych *et al.,* 1995). The inferred phoronid-spiralian relationship implies convergence between the larval and adult feeding apparatuses of the phoronids (and other lophophorate phyla) and those of larval enteropneusts and echinoderms (Halanych, 1996).

The phoronid actinotrocha differs strikingly from both spiralian and deuterostome larval forms in its large, mobile, and muscular oral hood, present throughout growth and development of the larva (Fig. 1). The anatomy and movements of this oral hood have been described, most recently in connection with descriptions of the nervous system (Hay-Schmidt, 1990a, 1990b; Lacalli, 1990). Though its structures have been studied extensively, the function of the oral hood remains unclear. Here we examine its role in the capture and transport of food.

Previous accounts of feeding by actinotrochas have focused on the operation of the lateral, laterofrontal, and frontal ciliary tracts on the tentacles. Paths of captured particles were compared with those observed for echinoderm larvae and prompted the suggestion that local reversals of groups of lateral cilia effected the capture of particles (Strathmann, 1973). It is also possible that the laterofrontal cilia of the tentacles play a sensory role in detection and capture of particles (Strathmann, 1973; Gilmour, 1978; Hay-Schmidt, 1989; Lacalli, 1990). The increase in number and length of tentacles during larval
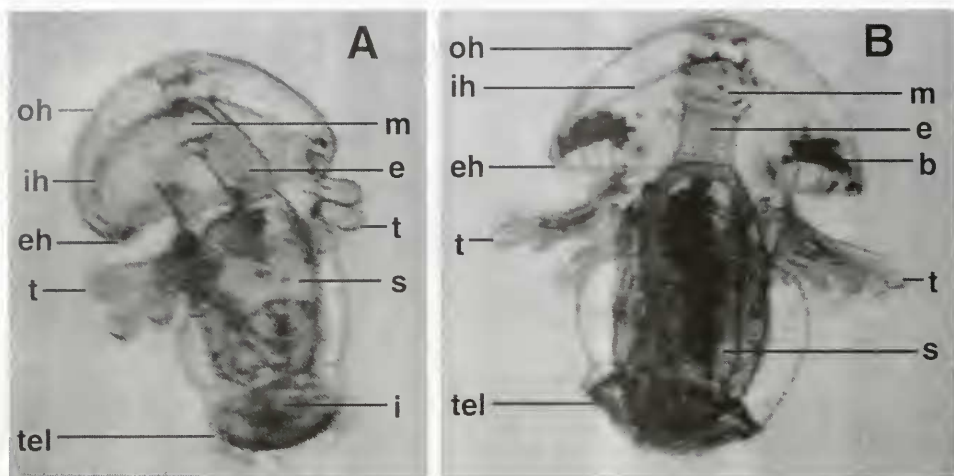
Figure 1. Actinotrochas of *Phoronopsis viridis* at the 12-tentacle stage in left and slightly dorsal view (A) and the 14-tentacle stage in ventral view (B). Labeled parts are mass of red blood cells (b), esophagus (e), edge of the oral hood (eh), intestine (i), inner wall of the oral hood (ih), mouth (m), outer wall of the oral hood (oh), stomach (s), tentacles (t), and telotroch (tel). The blood cells form paired masses in the hood and collar of the larvae at the 14-tentacle stage, and in Figures 2 to 5 should be distinguished from captured particles, such as the dark material in the stomach of the larva in (B).

development is like the increase in tentacles or lobes of other larval forms that use ciliary bands to capture food, and this increase has been interpreted as a means of increasing feeding capacity (Herrmann, 1979). These accounts all emphasize the role of cilia in capture of food.

Other observations suggest differences in the feeding mechanism. Actinotrochas can ingest large dinoflagellates and other prey that are large relative to the width of the tentacle (Lebour, 1922; Herrmann, 1976). Could the oral hood, in combination with propulsive and sensory cilia of the tentacles, provide a mechanism of particle capture that would account for these observations? The oral hood is lifted in response to a touch on the upper surface of the tentacles, and some ciliated cells of the tentacles are associated with nerve processes (Hay-Schmidt, 1989; Lacalli, 1990). These observations suggest that the tentacles might sense food and a lift of the oral hood aid in its capture. Here we describe transport of particles aided by movement of the oral hood, a process peculiar to the actinotrochas.

Materials and Methods

We examined actinotrochas of two types. Our first observations were of a single actinotrocha that was collected from the coastal plankton off Plymouth, England (English Channel), in June 1989. It matched descriptions of *Pho-*

ronis muelleri (Emig, 1982; R. L. Zimmer, pers. comm.), which occurs in this region. This larva was a more slender, graceful form than others that we observed.

Videorecordings were of actinotrochas from the northeastern Pacific Ocean. Several were collected from the plankton near Friday Harbor, Washington, USA (San Juan Channel), in the spring of 1991. These matched descriptions of the larvae of *Phoronopsis harmeri* (Zimmer, 1964). Zimmer described the anatomy of this larva in some detail under the provisional identification of Actinotrocha A. Others were collected from the plankton of Bodega Harbor, California, and may have belonged to *Phoronopsis viridis*, which is abundant there (Everett, 1991). These larvae resemble those of *P. harmeri*, and the species may be synonymous (Emig, 1982). Some of the actinotrochas collected near Friday Harbor were damaged in the posterior region, perhaps during collection, but swam and captured particles (Figs. 2 and 5). Those from Bodega Harbor were collected during a shorter plankton tow and were undamaged (Figs. 1, 3, 4).

Captured particles were the dinoflagellate alga *Prorocentrum micans* (about 20 μm), plastic spheres (polystyrene divinylbenzene of 5 to 30 μm diameter), and in a few cases Sephedex spheres from 25 to >65 μm diameter. Particles were added by Pasteur pipette at a wide range of concentrations.

All measurements of rates were for larvae observed and videorecorded with a compound microscope at room temperature (about 15° to 20°C). For estimates of velocities, times were obtained either from a time-date generator that labeled recordings to the nearest 0.01 s or from the interval between frames; distances were obtained from recordings of a stage micrometer. (Two videorecorders were used, resulting in different frame intervals: 60 frames per second for *P. harmeri* at Friday Harbor, and 30 frames per second for *P. viridis* at Bodega Bay. Because the greatest velocities included estimates from 30 images per second, the greater velocities estimated from sequences of *P. viriidis* did not result from differences in time intervals but rather from condition and behavior of larvae.) For most estimates of particle speeds, larvae were in chambers at least 1 cm in diameter by 0.5 cm deep, but because the larvae were often close to the upper or lower surface of the chamber, drag affected velocities, with greater effects expected at greater distance from a larva's motion. This chamber artifact is not so severe as to prevent comparisons of velocities close to moving cilia (Emlet and Strathmann, 1994). One estimate of the speed of particle transport was of a larva confined within the space in nylon plankton netting under a coverglass. Qualitative observations included larvae feeding in a water-cooled chamber under a dissecting microscope, with the larvae at least 1 cm from the nearest wall and temperatures close to ambient sea temperatures (about 10° to 15°C).

Results

Though different in form, actinotrochas from the plankton off Plymouth and those from Friday Harbor and Bodega Harbor used the oral hood in a similar way. Particles were carried past the actinotrocha in the current produced by the lateral cilia of the tentacles and a posterior ring of longer cilia (the telotroch). When a particle reached the area near the upstream side of the tentacles, the oral hood rapidly lifted, drawing the particle toward the mouth. When the hood lowered again, the particle remained beneath the oral hood (Figs. 2, 3, 4).

Hood lifts were more obvious in the larva from Plymouth (presumed to be *Phoronis muelleri*), but detailed quantitative observations were provided by videorecordings of captures by the larvae from Friday Harbor and Bodega Harbor (presumed to be *Phoronopsis harmeri* and *Phoronopsis viridis*). Hood lifts during some captures were inconspicuous but evident when videorecorded sequences were analyzed frame by frame. A hood lift followed a particle's contact with a tentacle—contact being defined as an approach within the length of the cilia. Close approach to the oral hood, as in Figure 2 at 0.1 s, did not trigger a hood lift. In all successful captures, the particle first came close to the tentacle and then the hood lifted. Hood lifts were sometimes slight, but transport of a particle from a tentacle to the vicinity of the mouth was accompanied by a hood lift in every sequence in which the positions of both particle and hood were visible.

The hood was often raised from an initial slit-like opening of about 10 μm or less (Fig. 2, from 0 to 0.2 s), to 50 μm or more (Fig. 2, from 0.5 to 0.7 s). Thus space under the oral hood increased when the oral hood lifted, and an influx of water must have occurred.

Variation in particle speeds during a capture indicates that the particle is initially being detained at the tentacle before being transported proximally along the tentacle, at a higher speed, during the hood lift. In the videorecorded captures, a particle's speed increased as it approached the tentacle; after making contact, it usually moved slowly for a brief period, often moving to the side of the tentacle before being returned to the frontal surface of the tentacle. Movement along the tentacle toward the mouth increased in speed when the oral hood lifted. Once beneath the hood, particles were moved slowly toward the mouth, often with a pause on the way. The initial detention at the tentacle indicates that a ciliary mechanism for the initial capture and concentration of particles operates before the hood is lifted. The hood lift then assists the capture by aiding transport toward the mouth.

Estimated speeds of particles during several captures confirmed this pattern of movement. In a capture by *Phoronopsis harmeri* (Fig. 2, particle marked by a bar), the maximum speed as the particle approached the tentacle was 1.1 mm s^{-1}. After contact there was a prolonged period of little proximal movement, with maximum speeds less than 0.5 mm s^{-1} in the interval from 0.2 to 0.5 s. During this interval (at about 0.4 s) the hood began to lift. As the hood continued to lift, the particle's speed increased to 0.9 mm s^{-1}. In a second observation on the same larva (not shown), the particle's speed was less than 0.5 mm s^{-1} just after it had contacted the tentacle but increased to 1.1 and then 1.3 mm s^{-1} as the hood lifted.

In the capture by *Phoronopsis viridis* in Figure 3, the particle's maximum speed as it approached the tentacle was 1.6 mm s^{-1}. The particle moved little between contact with the tentacle, at about 0.07 s, and the beginning of transport proximally, at about 0.08 s. Then the particle traveled proximally at about 1.5 mm s^{-1} during the next 0.02 s, with the hood just beginning to lift. Its speed increased to 2.7 mm s^{-1} during the next 0.03 s of transport to the base of the tentacle (at 0.13 s in Fig. 3). In the capture in Fig. 4 (same larva), the particle moved lateral to the tentacle at about 0.1 mm s^{-1} (from 0 to 0.20 s) and then moved proximally at about 0.5 mm s^{-1} (from 0.20 to 0.27 s) before a noticeable hood lift. When the hood lifted, the particle moved proximally at about 2.4 mm s^{-1} (in the interval between 0.27 and 0.32 s). In a third capture
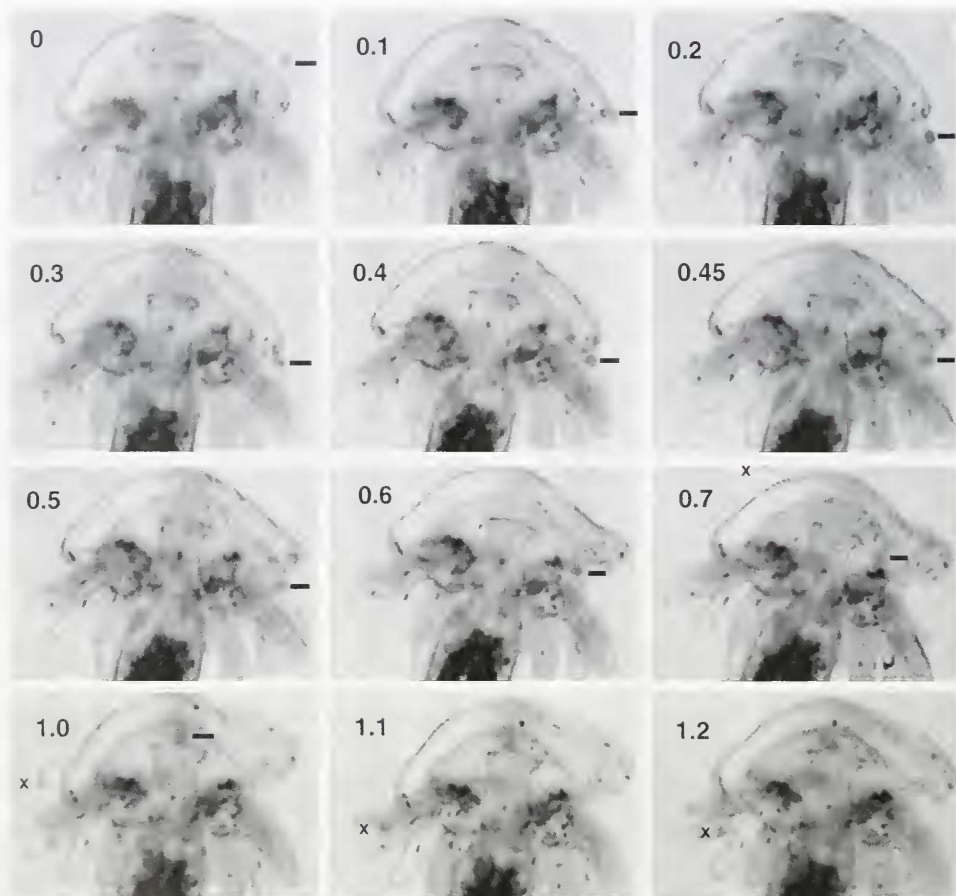
Figure 2. Two captures of the alga *Prorocentrum micans* by an actinotrocha (*Phoronopsis harmeri*) in ventral view. Numbers at the upper left of each frame are time in seconds from the first frame in the sequence. A black bar is to one side of the first algal cell captured on the viewer's right. An x is next to the second algal cell captured, on the viewer's left. The hood began to lift at about 0.4 s in the first capture, and the lift was nearly complete at 0.6 s. The cell had been drawn well under the hood at 0.7 s, and the second algal cell appeared (at the top of the frame). As the hood was lowered following the capture on the right, the second algal cell contacted a tentacle on the left at about 1.1 s, and a second hood lift and capture began on the left side. The width of the oral hood in the first frame is 480 μm. (This larva had sustained damage that extended the body posterior to the telotroch.)

(not shown and with hood movement out of focus and unrecorded), there was little movement during the first 0.2 s after the particle appeared near the tentacle tip, then movement lateral to the tentacle at less than 0.2 mm s^{-1} during the next 0.1 s, followed by proximal transport at 1.3 mm s^{-1} during the next 0.05 s. With another larva of

P. viridis (confined in a nitex mesh cage), a plastic sphere was held on the tentacle with little or no motion, then transported proximally along the tentacle at 0.25 mm s^{-1} during 0.1 s; it halted again for 0.1 s, and then increased speed to 0.6 mm s^{-1} as the hood lifted.

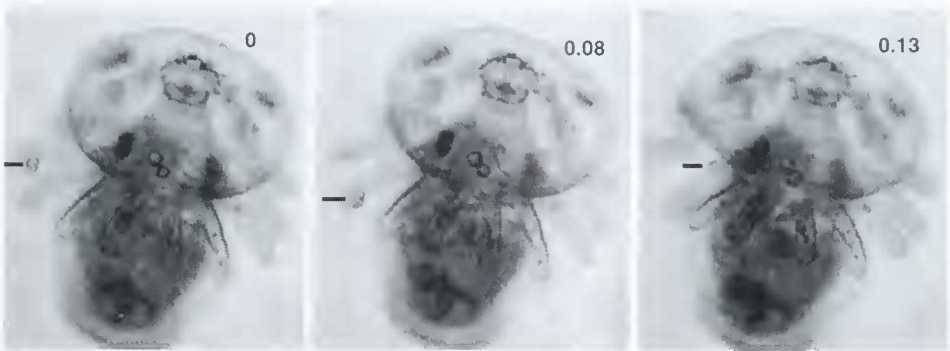Movements of particles corresponded even to irregular

Figure 3. Capture of a plastic sphere by an actinotrocha (*Phoronopsis viridis*) in ventral-anterior view. The black bar is to one side of the plastic sphere. Numbers at the upper right of each frame are time in seconds from the first frame in the sequence. The sphere contacted the tentacle near the tip and moved most of the length of the tentacle during the hood lift between 0.08 and 0.13 s. The width of the oral hood in the first frame is 460 μm.

lifting and lowering of the hood. When an actinotrocha lifted and lowered its oral hood in rapid succession, a particle moved proximally with each lift and distally with each lowering (Fig. 5). The motion of the particle in this and other examples exactly followed the motion of the hood.

The oral hood sometimes lifted when no particle was captured. When larvae were disturbed, they often raised the hood far beyond the elevation that accompanied particle captures. Lifting the oral hood may serve other functions, such as rejection of particles, escape, or defense, but our observations of the close correspondence between encounters with particles and elevation of the oral hood indicated a response to individual particles and a role in captures. The improbability of hood lifts and captures coinciding by chance alone was demonstrated by analysis of videorecorded sequences of 10-s duration with an actinotroch of *P. viridis* capturing plastic spheres 20 μm in diameter. In the first of these sequences, four plastic spheres passed close to the tentacles. Two passed with a hood lift and were captured. One passed with a hood lift but no capture. One passed without a hood lift. The observed proportion of particles passing that coincided with a hood lift was 0.75, and the proportion of particles captured was 0.5. The proportion of particles passing that would coincide with hood lifts by chance alone can be estimated by assuming that a capture or a hood lift each occurs within 0.3 s. The fraction of the interval with particles passing close to tentacles was then $4x(0.3 \text{ s})/(10 \text{ s})$ = 0.12, and the fraction of the interval with hood lifts was $3x(0.3 \text{ s})/(10 \text{ s})$ = 0.09. The probability of passage of a particle coinciding with a hood lift is then 0.011.

In a second sequence, also of 10 s but with a higher concentration of spheres, four spheres passed close to tentacles. Two were captured with hood lifts. One was not caught, but there was a hood lift. The fourth passed without a hood lift. There were also two motions of the hood with no particle in view. The observed fraction of particles passing that coincided with a hood lift was 0.75 and the observed fraction with captures was 0.5. Again, the expectation of this happening by chance alone can be estimated from the fraction of the interval with particles passing (about 0.12) and the observed fraction of the interval with hood lifts (about 0.15). The probability of a particle passing and a hood lift occurring together by chance is then 0.018. Even here the probability of the four passing spheres coinciding with hood lifts by chance is much lower than the observed proportion of coincident events. These calculations overestimate the probability of chance coincidence of hood lifts and captures because movements of hood and particle were more closely correlated than in the loose assumptions of our calculations, both in timing and in correspondence of the portion of the hood lifted to the position of the particle. The association of hood lifts and captures was not a chance occurrence.

When actinotrochas had ingested many particles, more particles passed the tentacles without a hood lift, and when they were disturbed, there were more hood lifts without the presence of a particle.

Lengths of cilia of actinotrochas of *Phoronopsis viridis* at the 14-tentacle stage were measured from video images. The four estimates of length of cilia on tentacles were 23, 25, 26, and 29 μm, within the range of cilium
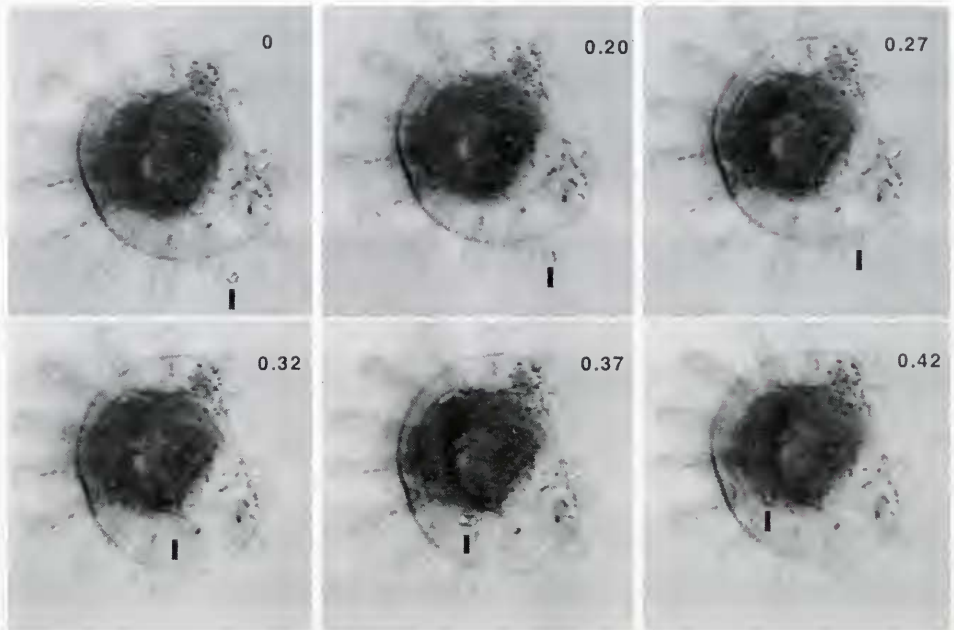
Figure 4. Capture of a plastic sphere by an actinotrocha (*Phoronopsis viridis*) in anterior view. The black bar is below the plastic sphere. Numbers at the upper right of each frame are time in seconds from the first frame in the sequence. The sphere approached and contacted the tentacle between 0 and 0.27 s. The hood began to lift at about 0.27 s, with the change in shape of hood evident at 0.32 s. Between 0.27 and 0.32 s the particle was drawn rapidly under the hood. It then moved more slowly toward the mouth while the hood remained lifted (at 0.37 and 0.42 s). The width of the oral hood in the first frame is 465 μm.

lengths observed for the adults of *Phoronis vancouver-ensis* (Strathmann, 1973). Estimates of cilium lengths from an arrested telotroch ranged from 51 to 57 μm (median 53 μm, $n = 7$). Estimates of cilium lengths from a beating telotroch ranged from 50 to 61 μm long (median 56 μm, $n = 7$). Tentacles (not including the cilium length) were 30 to 33 μm wide.

The largest particle found in the stomach of an actinotrocha of *P. viridis* was a Sephadex sphere 55 μm in diameter, but we did not test for the maximum size that could be captured and ingested.

Discussion

Roles of cilia and hood lift in capturing particles

The demonstrated role of the oral hood in transport of particles does not preclude the presence of ciliary mechanisms for particle capture similar to those in other larval forms. Our study focused on the role of the oral hood, but movements of particles suggest that cilia play an es-

sential role in capture and transport of particles. Cilia bring particles to the tentacles, initially detain them there, and aid in transporting them. The hood lift supplements a ciliary feeding mechanism but has not replaced it.

The actinotrochas appear to have two active responses to particles, with the ciliary one acting before the hood lifts. Cinefilms of particle capture by adult bryozoans have demonstrated that changes in the beat of the lateral cilia on the tentacles are associated with retention and transport of particles (Strathmann, 1982). One hypothesis of how the cilia of the tentacles of actinotrochas detain particles before the hood lifts is that particles approaching the tentacles induce the lateral cilia of the tentacles to arrest or reverse beat. This is consistent with the observed movements of particles to a position lateral to the tentacles on initial contact. There is a pause or slowing of movement of the particle at that location and then a transfer toward the frontal surface. Our videorecorded images of actinotrochas showed the paths of particles but were insufficiently clear to directly demonstrate changes in the beat of the cilia.
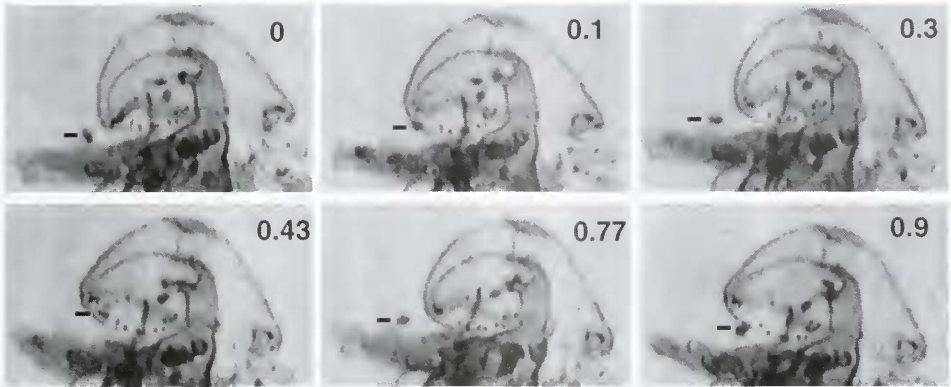
Figure 5. Movements of a cell of *Prorocentrum micans* in relation to repeated hood lifts by an actinotrocha. The view is of the dorsolateral side of the larva. The black bar is to one side of the algal cell. Numbers at the upper right of each frame are time in seconds from the first frame in the sequence. The hood had completed lifts at 0.1, 0.43, and 0.9 s. In each case the algal cell was drawn inward to the edge of the hood. Lowering of the hood had produced maximum outward excursions of the algal cell at 0.3 and 0.77 s. The scale was undetermined. (This larva had sustained damage that shortened the body posterior to the tentacles.)

A second hypothesis is that particles are halted by a sieve formed by stationary laterofrontal cilia, as observed for the cyphonautes larva of bryozoans (Strathmann and McEdward, 1986). The actinotrochas do have laterofrontal cilia (Hay-Schmidt, 1989), but our videorecorded images were insufficiently clear for direct observation of sieving by those cilia. The laterofrontal cilia of the tentacles may be sensory (Strathmann, 1973; Gilmour, 1978; Hay-Schmidt, 1989; Lacalli, 1990; Pardos *et al.*, 1991). Instead of or in addition to acting as a sieve, the laterofrontal cilia could detect the particles and trigger the hood lift.

Our observations do not separate the effect of a hood lift from the effect of the cilia in transporting particles toward the mouth. Raising the oral hood could change the currents generated by the cilia on the hood margin and other cilia of the oral region by changing distances from the body wall and other cilia. It is also possible that changes in ciliary beat coincide with movements of the oral hood. Thus changes in ciliary currents could contribute to a change in the movement of a particle when the hood lifts. However, the simplest explanation is that the hood itself is moving the water and the particle with it during its lift because (1) changes in the volume of the space under the hood must create a flow of water and (2) movements of particles corresponded exactly with lifts of the hood.

Particles are retained in some manner when the hood is lowered. The cilia beneath the hood may aid retention as the hood is lowered. Possibilities include sieving as a result of action and positions of cilia, changes in ciliary beat in response to particles, and changes in beat coordinated with movement of the hood.

Implications for quantitative performance

The hood lift of the actinotrochas is distinctive. Does it confer distinct advantages in either range of available foods or maximum clearance rates?

The hood lift may permit capture of more active prey than is possible when captures are by cilia alone. The greatest velocities of particles transported by hood lifts were 2.7 and 2.4 mm s^{-1} in our study. Other measured velocities were slower and overlapped estimates for transport by cilia alone on animals with ciliary bands like those of actinotrochas. These estimates are 1.2 mm s^{-1} for a particle transported down the arm of a pluteus (Hart and Strathmann, 1994), about 0.7 mm s^{-1} in the food groove of the hemichordate *Planctosphaera pelagica* (Hart *et al.*, 1994), and 0.75 to 1.55 mm s^{-1} for transport down a bryozoan's tentacle (Strathmann, 1982). In the mitraria of oweniid polychaetes (a larva with opposed bands but simple cilia), transport in the food groove was 0.1 to 0.4 mm s^{-1} (Emlet and Strathmann, 1994). Transport by either hood lift or ciliary tracts should be adequate to overcome the 0.1 to 0.5 mm s^{-1} swimming speeds of dinoflagellates (Sournia, 1982). Other potential prey swim faster. Reported swimming speeds for a variety of ciliates range from 0.5 to 1.2 mm s^{-1} (Sleigh and Blake, 1977).

These comparisons suggest that the faster transport with some hood lifts could extend the range of prey that (after the initial encounter) can be retained and transported to the mouth.

The actinotrochas may capture prey larger than those available to other larvae with similar ciliary bands. Reported gut contents include armored dinoflagellates, tintinnids, diatoms, occasional bivalve and gastropod larvae, and a copepod egg (Lebour, 1922). Actinotrochas of *Phoronis muelleri* filled their guts with the armored dinoflagellate *Peridinium trochoideum* and even attempted to ingest smaller actinotrochas (Herrmann, 1976). In our study, the largest particle ingested by *Phoronopsis viridis* was only 55 μm, but this is 10 μm larger than the largest spheres ingested by bryozoan and echinoderm larvae under similar conditions (McEdward and Strathmann, 1987). The muscular oral hood of the actinotrocha provides a mechanism for capturing large prey, but such prey can also be captured by some ciliary mechanisms. Some types of small ciliated larvae ingest large particles. These include several types of polychaete larvae that do not use the opposed-band feeding mechanism (Strathmann, 1987). For example, a trochophore of a polynoid polychaete, 18 days old and thus only about 130 μm long, was able to capture a centric diatom 60 μm in diameter (Phillips and Pernet, 1996). The hood lift may provide capture of types of prey that would otherwise be unavailable, but this hypothesis was suggested, not tested, by our study.

Does capture by a hood lift permit a greater maximum clearance rate? The maximum clearance rate of actinotrochas depends on diversion of a particle and a small quantity of surrounding water from the much larger volume of water that flows within range of its sensors. When there is no particle to be caught, water flows posteriorly in the currents produced by the lateral cilia of the tentacles and by the posterior ring of cilia, but when a particle is detected by cilia or other structures on the tentacles, the oral hood lifts and the particle is captured together with a small quantity of water. Water may be eliminated as the oral hood is lowered, but the greatest concentration of suspended food comes not from filtration but from sensing and capturing individual particles. Such mechanisms have been termed scan and trap (LaBarbera, 1984) or active response (Strathmann, 1987) methods of suspension feeding. Particles contacting the tentacles anywhere from near the base (Fig. 2) to near the tip (Fig. 3) can be captured. Thus the maximum clearance rate depends on three distinct features: the speed of the water flowing past the tentacles, the length of the tentacles, and the distance from the tentacles at which particles are sensed. Is there evidence that the actinotrocha has evolved an unusual capability in any of these three components of clearance rate, as a possible result of transport aided by a hood lift?

If the hood lift permits captures from a faster current, then it could confer a greater clearance rate than is possible with ciliary bands alone. The actinotrocha might achieve a faster swimming and feeding current by additional propulsion from its telotroch, a posterior ring of longer cilia (Nielsen, 1987). Also, the lateral cilia themselves might produce a faster current. Our observations were not designed to measure velocities of particles approaching the tentacles, but the observed speeds of 1.1 and 1.6 mm s^{-1} were similar to the mean speeds of 0.8 to 1.4 mm s^{-1} recorded for a variety of echinoderm larvae (Hart, 1996). If actinotrochas produce feeding currents that are faster than those of similar larval forms, we failed to observe them. Also, in at least some captures the particle is detained on the tentacle for a brief period before the hood lifts. In these cases processes other than the hood lift are responsible for initially detaining particles (as discussed above).

Has capture aided by the oral hood resulted in evolution of a greater total length of tentacles and ciliary bands than in similar larval forms? The larva in Fig. 4 had a total length of tentacles of about 2.1 mm, if one assumes that all tentacles are parallel to the plane of focus; and because there are ciliary bands on both sides of each tentacle, the total length of band is about 4.2 mm. Echinoderm larvae also develop through a stage with this band length (Hart and Strathmann, 1994; Hart, 1996). Although differences in body organization prevent exact comparisons of body size, some echinoplutei with 6 to 8 arms are similar to this actinotrocha in both body length and ciliary band length (McEdward, 1984, 1986). The total length of lateral ciliary band of this actinotrocha is not extraordinary for larvae of its size.

It is possible that contact between a particle and the laterofrontal cilia triggers a hood lift, and the laterofrontal cilia may extend farther from the tentacle than the lateral cilia (Strathmann, 1973), thereby increasing the clearance rate. This hypothesis is subject to the same objection that particles can be detained at the tentacles before the hood lifts. If particles passing at a greater distance are retained, other processes than the hood lift may be responsible for this capability.

The hood lift does not appear to permit greater clearance rates, although there remains the possibility that the hood lift permits capture of prey that are so swift that it is the prey's speed rather than the actinotroch's speed that determines frequency of encounters.

Contrast with other larval forms

The use of muscles in connection with capture or transport of particles to the mouth is not known for other larvae that capture particles upstream from bands of simple cilia. A functional and structural equivalent of the oral hood is

unknown for the larval forms most closely resembling the actinotrocha. In the larvae of bryozoans, enteropneusts, and echinoderms, muscular movements pass food through the gut after it has been concentrated in the oral cavity by cilia (Strathmann, 1971, 1973; Strathmann and Bonar, 1976). Muscles of larval echinoids and ophiuroids dilate the mouth as an aid to rejecting particles, and dorsal muscles in asteroid larvae flex the larval body, which both opens the oral region as an aid to rejecting particles and changes direction of swimming (Strathmann, 1971). A functional analogue of transport aided by a hood lift is unknown for larvae of other lophophorates, of echinoderms, or of enteropneusts.

Transport aided by the oral hood also differs from particle capture by larvae with the opposed-band mechanism, which is widespread among larvae of the spiralian phyla. Veligers and trochopores with opposed bands rely on the action of cilia rather than on muscles for capture, transport, and rejection of particles (Werner, 1955; Strathmann *et al.,* 1972; Gallager, 1988; Hansen, 1991). Polychaete larvae and their feeding mechanisms are diverse, however, and muscles aid capture or transport of food in some families. Reported examples include flexing of the chaetopterid larval body to ingest a mucous net (Werner, 1953), and capture of animal prey by tentacles of magelonid larvae (Wilson, 1982), but these structures and activities do not resemble the action of the actinotrocha's oral hood.

The action of the actinotrocha's oral hood in feeding explains a prominent and peculiar feature of a distinctive larval form. The large number of muscles in the oral hood is also distinctive and may be required for the local lifts in response to particles contacting different tentacles. There is no known analogue in larvae of other phyla.

Adult forms also provide no close analogue to the hood lift of actinotrochs. Tentacle flicks by adult bryozoans aid transport of particles toward the mouth (Strathmann, 1982), but this does not appear to be a suction mechanism. The structure is not homologous to the actinotrochas hood, and the mechanism is not analogous to the hood lift. (The tentacles of actinotrochas often move during particle capture, but it is not apparent that these twitches aid transport of particles.) Production of a feeding current by flapping one valve has been suggested for extinct strophomenide brachiopods, but the proposed function of flapping was production of feeding currents, not transport of particles from tentacles to mouth (Rudwick, 1970).

Suction by the oral hood of actinotrochas invites comparison with suction and ram feeding by fishes, but the particle velocities associated with hood lifts in our observations are far lower. A particle's velocity relative to the mouth of a small fish can be the combined effects of ram (movement of the fish toward the particle) and suction (Coughlin, 1994). For carp of 5 to 8 mm body length, the

movement of prey relative to the mouth can be 260 mm s^{-1} (Drost, 1987), about 100 times the speed at which prey are moved by the actinotrocha's hood lift. The Reynolds number for flow produced by an actinotrocha lifting its hood is less than one. Thus, in contrast to ram and suction by small fish, viscous forces exceed inertial forces.

Acknowledgments

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